

Flying Slower: Floor Pattern Object Size Affects Orthokinetic Responses During Moth Flight to Sex Pheromone

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Revised: 5 March 2014 / Accepted: 31 March 2014 /
Published online: 30 April 2014

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Abstract Previous studies with Oriental Fruit Moth (OFM, *Grapholita molesta*) and *Heliothis virescens* males flying upwind along a pheromone plume showed that they increased their upwind flight speed as they flew higher above striped floor patterns and, for OFM, to a similar degree over dotted floor patterns. This response pattern has been demonstrated in another moth species, *Epiphyas postvittana* and in a beetle, *Prostephanus truncatus*. In all cases the role played by the change in angular size of the wind tunnel's ventral floor pattern was not assessed. In the present study we specifically addressed this question with a systematic examination of moths' flight control over different sizes of transverse stripes and dot patterns ranging down by halves from 5 to 0.625 cm and a blank white floor as a control, and showed that OFM males fly faster upwind and along their flight paths over floor patterns of decreasing size. Increased speeds over striped patterns were evident as stripe width decreased below 2.5 cm, whereas moths did not increase their flight speed over dot patterns until dot size had decreased to less than 1.25 cm. Another flight component that the moths can actively control, their course angles, was unchanged above both patterns, except for moths flying over 5 cm stripes. Turning frequency and interturn distances were mostly unchanged or offset each other, negating any effects on upwind progress. As in an earlier study examining flight speeds at three heights above floor patterns of three densities, the moths' changes in speed appear to be exclusively affected by changes in their orthokinetic response to the size of the floor pattern objects.

Keywords Flight speed · visual patterns · moths · sex pheromone · vision

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Introduction

The odor-mediated upwind flight of insects toward attractive odor sources to locate important resources (e.g., mates or food) has long been known to involve an optomotor anemotaxis (Kennedy 1939; Kennedy and Marsh 1974; Kennedy; 1977), which is the reliance on visual patterns to ensure that progress is made when orienting upwind. Most published studies focused on the response of male moths to wind-borne female sex pheromone (Cardé and Minks 1997), although this behavior has also been studied with respect to other odors (e.g., Haynes and Baker 1989; Willis and Arbas 1991). A working hypothesis for the control algorithm underlying this behavior, encompassing optomotor anemotaxis and other mechanisms (see Baker 1989, 1990; Cardé 1984, 1986), states that male moths have an endogenous central nervous system (CNS) counterturning generator, activated by contact with a wind-borne attractive odor (Kennedy et al. 1980, 1981). This putative CNS counterturning generator initiates “zigzagging” flight tracks which are directed toward the source (positive anemotaxis) by the presence of wind (Baker et al. 1984). These behaviors result in flights we typically observe from plume tracking male moths (Kennedy 1983). Zigzagging flight also continues for some time in the absence of pheromone as well (e.g., Kennedy et al. 1980, 1981; Baker and Kuenen 1982), primarily documented as crosswind casting with no net progress upwind or downwind (Kennedy 1983; however, see also Kuenen and Cardé 1994). The taxis (steering) component(s) of test insects’ tracks are largely the focus of these studies whereas the orthokinetic (movement) component is more typically cast in a secondary role.

The control algorithm described above accounts for the general shape of the upwind flight path of male moths toward female sex pheromone sources; however, these moths alter specific parameters of their flight in response to changes in plume concentration (Cardé and Hagaman 1979; Kuenen and Baker 1982b), plume structure (Mafra-Neto and Cardé 1994; Vickers and Baker 1994), odor ratios (Willis and Baker 1988), wind speed (Cardé and Hagaman 1979; Kuenen and Baker 1982a; Willis and Cardé 1990) and visual cues (Foster and Howard 1999; Kuenen 2013). The importance of visual cues for insect steering upwind, though long ago recognized (Kennedy 1939), has largely been ignored as a stimulus variable that influences flight responses by male moths flying toward pheromone sources. However, the regulation of the orthokinetic responses (for flying insects, the regulation of their flight speed) (Fraenkel and Gunn 1961; Kennedy 1978) is critical for making progress toward an attractant source. Kennedy’s (1939) demonstration of the use of visual cues for upwind orientation (steering) and his extensive field observations of locust swarms at various elevations (Kennedy 1951) led him to develop an “optomotor theory of behavior in wind”. Specifically, he hypothesized that flying insects control their airspeed (Fig. 1) using a servo mechanism in order to maintain a ground speed that produces a constant angular velocity of image motion across the retina. Kuenen and Baker (1982a) demonstrated that moths flying upwind toward a pheromone source flew faster at greater heights than at lower heights above the floor of their wind tunnel, which qualitatively supports Kennedy’s hypothesis. However, the moths did not increase their speeds enough to maintain a constant angular velocity of image motion over their eyes. This discrepancy between measured angular velocity and the hypothesized outcome was attributed to other competing visual cues in the experimental setup. An increase in speed with

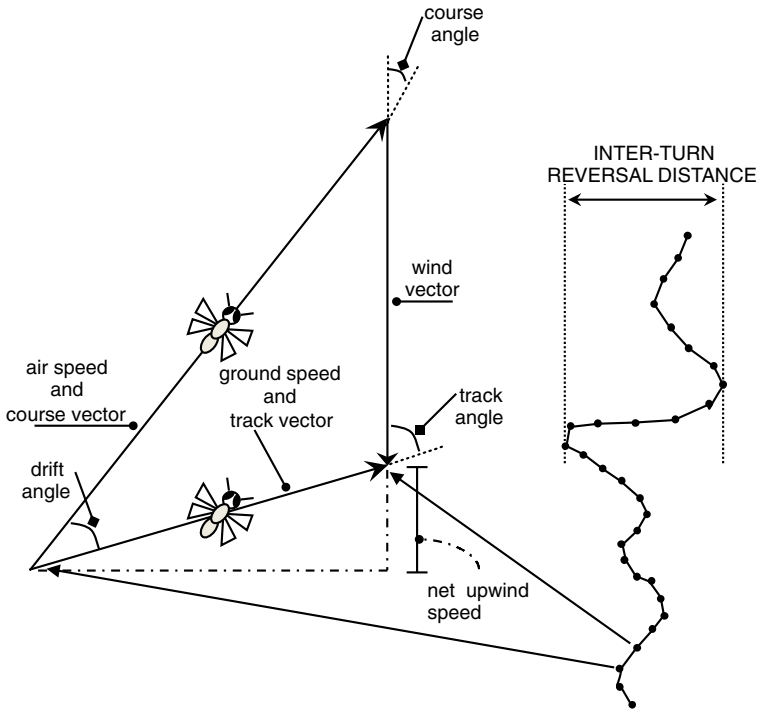


Fig 1 Schematic representation of a flight track denoting inter-turn reversals and parameters and terminology from the triangle of velocities (after Marsh et al. 1978) used for analysis and description of *G. molesta* tracks. Airspeed: speed of males through the air resulting from the wind and their ground speed. Ground speed: speed of males along their actual track. Track angle: angle flight vectors (see text) with respect to the upwind direction (0°). Drift angle: deviation of a moth's course angle to its observed track angle due to displacement by the wind. Wind is from the top of the figure. Net upwind speed is added to indicate moth's progress toward the pheromone source

increased flight height was also demonstrated with the beetle *Prostephanus truncatus* by Fadamiro et al. (1998). In both studies, the insects were less responsive to experimental movements of a ventral floor pattern when flying higher above them, suggesting that other visual cues present in the flight tunnel or assay-room play a greater role in regulating their flight toward the pheromone source. Foster and Howard (1999) found that the lightbrown apple moth (LBAM, *Epiphyas postvittana*) also increased their ground speed when flying higher above their wind tunnel's dotted floor pattern. These three studies lend support to Kennedy's (1951) "optomotor theory" for speed control based on image flow across the eye surfaces, but each study overlooked the fact that the apparent size (angular size) of the visual cues in these experiments was an uncontrolled variable.

This led us to test the speed and steering changes used by OFM during their flights over floor patterns of various size (stripes and dots) at a fixed flight height. We show here that male OFM flying upwind toward a pheromone source over dotted and transverse striped ventral floor patterns exhibited a positive orthokinetic response, that is, an increased ground speed, when the size of the patterns were small; subtended angles of ca. 14° or less were required to elicit these changes. Steering and turning components of these flights changed little as flight speeds increased.

Materials and Methods

Insects Oriental fruit moths, *Grapholita molesta* (Busck) (Tortricidae), were reared on a wheat germ and agar-based diet (Yokoyama et al. 1987). All life stages were maintained at 26 ± 2 °C on a 16:8 light:dark cycle. Males were separated from females in the pupal stage. Adult males were isolated from females at all times and were segregated daily by age. All pupae and adults were held at ca. 85 % RH and adults had continuous access to an 8 % sucrose solution.

Flight Tunnel The flight tunnel has a $98 \times 98 \times 240$ cm working section, open at the downwind end with air pushed through the tunnel by a variable speed fan (Kuenen and Rowe 2006). The tunnel is constructed of acrylic-plastic panels affixed along their long edges to aluminum rails bent 90 ° in cross section, and to welded box-section aluminum exterior frames at each end. Tunnel access is through the downwind end or through one side composed of two 130 cm long door panels that slide parallel on closely apposed rails. Wind is provided by a variable speed DC-motor/fan with a rectified voltage-controller. Air is ducted to the upwind end of the tunnel by a flexible, polyethylene-sheeting (0.3 mm in thickness) tube between the fan and the tunnel's upwind aluminum frame, and passes through two layers of charcoal-and zeolite-impregnated filter material (Quality Filters, Robertsedale, Alabama), held in individual aluminum frames, before entering the working section of the tunnel; filter material is replaced twice yearly or earlier if reference test flights are abnormal. These filter layers remove volatile chemicals from the air (Heath and Manukian 1992) and reduce large-scale air turbulence. A third aluminum frame holds a layer of white or black muslin fabric that further smoothes the air flow and the color is chosen to enhance visibility of the moths depending on the species being tested and the lighting level in the tunnel.

Pheromone laden air/plumes are exhausted to the outside by a 20 cm-dia. airduct (air speed 3.6 ms^{-1}), whose center is aligned with the height of the pheromone release point. All remaining air passing through the tunnel is re-circulated through the assay room. Pheromone plumes from a 9×19 mm rubber septum (long side vertical) flowed horizontally straight down the tunnel with near-equal horizontal and vertical spread to ca. 10 cm diameter, as visualized by smoke plumes. Lighting in the assay room was from above by four 40-W fluorescent tubes (120 Hz) placed 20 cm to the side and 85 cm above the top of the tunnel. These lights were supplemented by 20 clear 40-W incandescent bulbs, 10 spaced equally along both sides of the tunnel 10 cm below the fluorescent bulbs. Illumination from both sets of lights was reflected from a layer of white expanded polystyrene directly above the tunnel, whereas direct light from the bulbs was blocked from the tunnel by aluminum foil. Light intensity at the 5 cm flight height was 345 lux from above, 155 lux from the floor, 215 lux from the white wall behind the tunnel and 160 lux from the clear, opening side of the tunnel as measured by a FisherBrand™ light meter, model 06–662–64 (Fisher Scientific, Friendswood, Texas).

Four-to six-day-old males were tested during the last hour of photophase and the first hour of scotophase, which is the time of their optimal responsiveness to pheromone (Baker and Cardé 1979a). The moths were conditioned to tunnel wind and light conditions for at least 60 min prior to their individual release from a small aluminum screen cone hand-held in the center of the pheromone plumes. This position was

determined during previous smoke visualization of the plume. Moths' flight height was controlled by suspending the pheromone source (see below) on a thread from the top of the tunnel. The hook was positioned on the longitudinal midline of the tunnel 30 cm from the upwind end of the tunnel. The moths maintained their flight height close to the center of the horizontal plume axis (vertical movements were rarely seen to exceed the plume boundaries) and their lateral flight movements were typically 5–10 cm wide and centered on the plume axis, within the range reported previously for plume tracking OFM males (Kuenen and Baker 1982b; Baker et al. 1984, Willis and Baker 1988).

Wind speed was maintained at 75 cm s^{-1} as measured with a Kurz hot-wire anemometer (model 491; Kurz Instruments, Monterey, California) that was calibrated by timing smoke puffs through a 1.2 m section of the tunnel. During flight tests, the tunnel room conditions were maintained at 23–25 °C and 45–60 % RH.

Flight Track Recording and Analysis Upwind flight tracks of the moths were recorded in plan view from above at 30 frames s^{-1} (fps) with a Photron FasCam PCI (San Diego, CA; www.Photron.com) digital video camera. The moths' flight tracks (30 fps) were then digitized with Mantis2 software (Synceros Inc., Ithaca, New York). The camera head and lens were oriented vertically above the tunnel ceiling (the lens protruded 5 cm through a hole in the expanded polystyrene-covered room ceiling) providing a 65 cm field of view at the 5 cm height. The upwind end of this 65 cm section was 60 cm from the pheromone source.

To obtain mean course angles, track angles, drift angles, airspeeds and ground speeds, calculations were based on the triangle of velocities method (Fig. 1; Kennedy 1939; Marsh et al. 1978). Data files [consecutive (0.333 s) x, y coordinate pairs for each flight track] were analyzed with a computer program developed by Kuenen and Baker (1982b); (see also Charlton et al. 1993; Kuenen and Cardé 1993, 1994; Kuenen and Rowe 2006) for calculation of the moths' movement parameters along each track vector (track segment between consecutive locations). In the present study, the mean track angle was calculated for an entire flight path by calculating the mean 'x' and 'y' displacements from all the vectors of a given flight path (using the absolute values for the crosswind component), yielding a mean resultant track vector. This procedure was followed to avoid the error inherent in calculating arithmetic means directly from angle measurements (Batschelet 1981), especially when vector lengths are not equal, as is typical during the dynamic free flight of these male moths (Willis and Arbas 1998). Subsequent calculations and analyses of movement and steering components of males along their flight paths were also based on this resultant vector and the wind speed vector (Kuenen and Cardé 1993, 1994). A program subroutine determined the turn apices and calculated inter-turn distances and durations (Kuenen and Rowe 2006). Turn apices were defined as the points where males changed direction across the wind line (Kuenen and Cardé 1993, 1994) and inter-turn reversal distances were taken as the lateral displacement between the apices of consecutive turns (Kuenen and Baker 1982b).

Pheromones The female sex pheromone of *G. molesta* consists of 5.9 % (*E*)-8-dodecenyl acetate with 3.8 % (*Z*)-8-dodecyl alcohol (Cardé et al. 1979) in (*Z*)-8-dodecenyl acetate (Roelofs et al. 1969). These compounds were purchased from

Bedoukian Research (Danbury, CT, USA), all nominally $\geq 97\%$ pure. Stock solutions of each compound were made in hexane (10 mg/ml) and then mixed in the appropriate ratios. Serial dilution of this mixture yielded solutions for loading onto gray rubber septa (West Co., Lionville, PA, USA item # 1888, sleeve type, 9×19 mm). Ten μg of this mixture in 10 μL hexane was applied to the inside bottom of the large end of a rubber septum. The ratio of the pheromone components (Baker and Cardé 1979b) were verified by gas liquid chromatography on a DB-5 column in an HP 6890 gas chromatograph (Agilent Technologies, Palo Alto, CA, USA after Baker and Roelofs 1981). The ratios of compounds in our solution were 6.5 % (*E*)-8-dodecenyl acetate with 4.9 % (*Z*)-8-dodecyl alcohol in (*Z*)-8-dodecenyl acetate. Overall purity was $>95\%$.

Experimental Design Moths tracked a pheromone plume emanating from a rubber septum suspended by a white thread 5 cm above the tunnel floor. These upwind flights were over white tunnel floors with no patterns or patterns composed of stripes or dots on a white floor. Striped patterns were alternating red and white stripes with individual stripe widths of 0.625 cm, 1.25 cm, 2.5 cm or 5 cm. These absolute sizes yield pattern wavelengths (one red plus one white stripe) of 14.2° , 28° , 51° , and 90° when viewed directly from above from the 5 cm elevation of the pheromone lure. The angular subtense of patterns seen by the moth will vary with actual flight height and will be smaller when not viewed directly from above due to foreshortening. The diameters of the dotted pattern matched the widths of the stripes and were placed pseudo-randomly on the white paper; the number of dots placed on the floor was adjusted to yield a surface area that was 50 % red to match the 50 % red in the striped patterns (e.g., we used 38,331 dots of 0.625 cm diameter to obtain a 50 % red floor covering). The floor patterns were printed with a poster plotter (HP Design Jet 4500, Palo Alto, CA, USA) on white paper (HP cat. # Q1406A) that was trimmed to 98 cm and then laid on the floor inside the tunnel.

Statistical Analyses Tests were conducted in a randomized complete block design with three moth flights per floor pattern per day. Tests were conducted over the course of 8 days with all patterns tested once each day. Thus, 24 moths were flown over each of the eight ventral object-size patterns and a blank white floor, resulting in a total sample size of 216 moth tracks for the entire experimental design. A two-way analysis of variance and mean separation tests were conducted with PROC GLM and Tukey's HSD test, respectively in SAS (SAS 2010 version 9.1, Cary, NC, USA).

Results and Discussion

The moths flew uptunnel (net speed) fastest ($P < 0.05$; Fig. 2) over the blank floor and over patterns with the smallest stripes or dots, with speed decreasing as the moths flew over larger floor pattern objects. There were no significant differences in their speeds between stripe- or dot-size pairs (Fig. 2). Changes in net uptunnel speeds were mostly paralleled by actual ground speeds. Similarly, the airspeeds of these insects also paralleled the changes in their net speeds (Fig. 2). Moths can actively control two

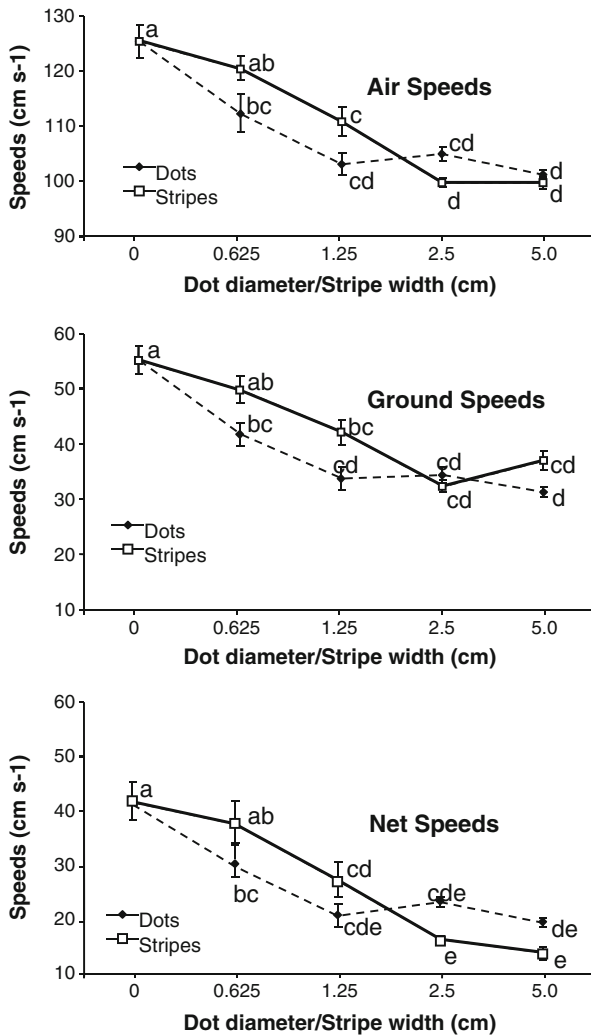


Fig 2 Mean (\pm SEM; $n=24$) airspeeds, ground speeds and net upwind speeds of *G. molesta* flight tracks during upwind flight towards pheromone over nine floor patterns. Means along each pair of lines having no letters in common are significantly different (Tukey’s HSD test; $P<0.05$)

aspects of flight: thrust and orientation (Marsh et al. 1978). The negative orthokinetic response, i.e., decreased ground speeds, exhibited by moths flying over larger floor-pattern objects is due to reduced thrust. Thinking further through the relationships in the triangle of velocities (Fig. 1), it becomes clear that the moths’ course and track angles could not have changed substantially given the close paralleling of the ground speed and airspeed. Indeed, the course angles, the other actively controlled flight parameter, exhibited only one significant difference among all the test treatments - moths flying over 5 cm stripes (Fig. 3). Moths flying over the dot patterns exhibited nearly identical course angles regardless of dot size. The reduced flight speed of moths steering similar course angles over larger floor pattern objects led to the moth being pushed more off course leading to greater track and drift angles (Fig. 3), most notably over the larger-

stripe floor patterns as their flight speeds dropped more than moths flying over larger-dot floor patterns.

In addition to the parameters delineated in the triangle of velocities (Marsh et al. 1978), moths can change the frequency of their crosswind turns and their interturn distances. Moths flying over the dotted floor patterns exhibited a linear increase in turn widths as they flew over larger dots, but this increase was only significant for 5 cm dots compared to the blank white floor and the smallest, 0.625 cm dots (Fig. 4). The turn frequency of these moths changed in the opposite manner from turn widths, reducing in number as they flew over larger dots (Fig. 4), again in a linear mode with increasing dot size. Moths flying over striped patterns showed no pattern of change in turn widths with changes in stripe width (Fig. 4), and similar to the moths flying over dots, their small changes in turn frequency were nearly a mirror image of their changes in turn distances. For OFM, changes in turn rates and/or inter-turn

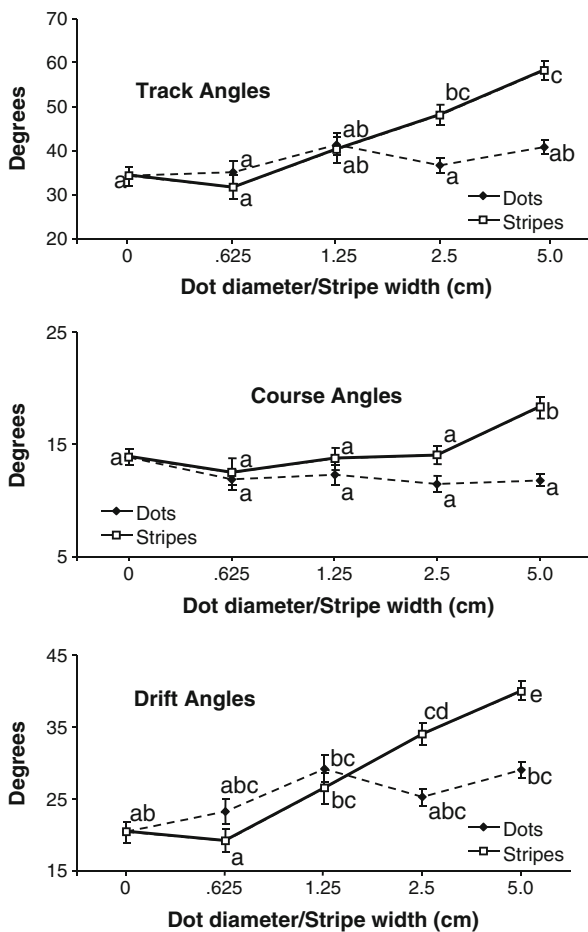


Fig 3 Mean (± 1 SEM; $n=24$) track angles, drift angles and course angles of *G. molesta* flight tracks during upwind flight toward pheromone over nine floor patterns. Means along each pair of lines having no letters in common are significantly different (Tukey's HSD test; $P < 0.05$)

distances, can be indicative of changes in their flight speed (Kuenen and Baker 1982b); however, we only saw a significant difference in the moths' turn rates and inter-turn distances in response to changes in dotted floor-pattern object size (Fig. 4).

Insects flying higher over fixed patterns in wind tunnels have demonstrated higher speeds than their counterparts flying lower in the tunnel. This has been documented for *G. molesta* and *H. virescens* (Kuenen and Baker 1982a); *E. postvittana* (Foster and Howard 1999); *P. truncatus* (Fadamiro et al. 1998). However, in all these studies the change in the subtended angular size of the fixed floor pattern (with increased flight height) was not controlled as a possible effector of flight speed increase. As an insect flies higher over a pattern of fixed size, the angular subtense of pattern objects decreases. Conversely, here, when we experimentally decreased the subtended angle of the floor pattern objects at a single flight height, moths also increased their flight speed. We observed that smaller object size leads to greater flight speed but we also recorded only limited effects of pattern size on the moths' steering and turning maneuvers as they altered their flight speed.

It is typically stated that only thrust and steering can be actively controlled by free-flying insects [true for the triangle of velocities (Marsh et al. 1978)], but insects can also alter the tempo of their crosswind turns which, along with regulated thrust, can affect the distance an insect flies, which in turn when combined with steering and thrust can affect the net upwind speed an insect flies. The paucity of differences in steering and turning parameters as moths flew above either striped or dotted floor patterns combined with the significant increase in ground speed above smaller floor-pattern objects led to increases in net upwind speed. These data support the contention of Kuenen (2013) that previously documented increases in ground speed among higher flying insects

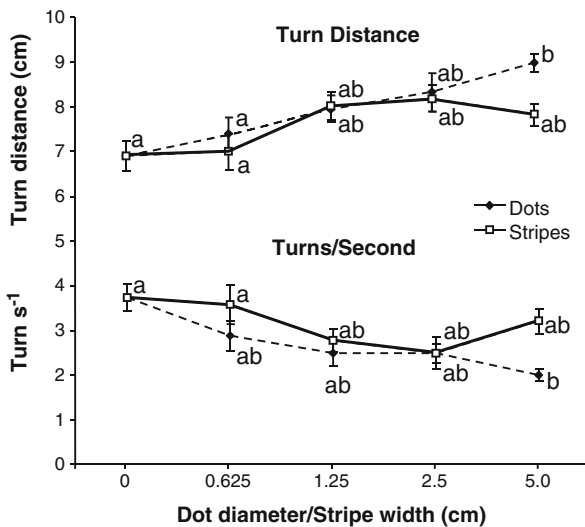


Fig 4 Mean (± 1 SEM; $n=24$) turn rates and inter-turn reversal distances of *G. molesta* flight tracks during upwind flight toward pheromone and over nine floor patterns. Means along each line having no letters in common are significantly different (Tukey's HSD test; $P < 0.05$)

appears due almost exclusively to a positive orthokinetic response to the decreased angular subtense of the ventral visual cues as flight height increased.

For OFM males the actual change in visual cue sizes at one height (this study) and induced changes in visual cue size by changing flight height (Kuenen 2013) led to similar orthokinetic responses with little change in steering or turning maneuvers. Lightbrown apple moths (LBAM) also increased their ground speed and made wider turns when flying higher above a dot floor pattern; however, their net speed upwind was not significantly different from that at lower flight heights (Foster and Howard 1999). Although Kuenen (2013) examined effects of pattern density on OFM's flight responses, Foster and Howard (1999) used a very low pattern density (<10 % floor coverage) and used larger 10 cm dots than the 5 cm dots used for OFM. The resulting paucity of visual cue edges may have contributed to the wider turns by LBAM and was also noted among OFM males when they flew over low density (12.5 % coverage) floors with dot patterns, but not striped floor patterns (Kuenen 2013). None of these turning response data are available for *H. virescens* (Kuenen and Baker 1982a) or *P. truncatus* (Fadamiro et al. 1998).

The moths in this study did not maintain a constant angular velocity of image motion as predicted by Kennedy (1951). Earlier experiments with OFM flying at several heights, also did not quantitatively support Kennedy's hypothesis (Kuenen and Baker 1982a; Kuenen 2013). Although this study was not a direct test of that hypothesis, the large increase in the moths' flight speeds as they flew over small floor-pattern objects does mimic, to some extent, the effect of flying higher above fixed-size floor objects. The net speed changes toward the pheromone source were due almost entirely to changes in the orthokinetic output of the test moths with nearly no changes in steering or turning. As our OFM moths flew over smaller object-pattern sizes, they would have been able to see more pattern/object edges on the tunnel floor, as they did when flying higher above fixed-size-pattern-objects (Kuenen 2013). In other words, at this study's 5 cm flight height, the effect on flight speed of reducing floor-pattern sizes by halves, was similar to the effect of increasing flight height by doublings (Kuenen and Baker 1982a; Kuenen 2013). Further tests with OFM males flying at multiple heights over floor patterns spanning a broad range of angular subtense have been conducted; the results support the work here, and further, indicate that males' flight speed may be regulated by maintenance of visual cue contrast frequency rather than maintenance of visual cues' angular velocity (Kuenen & Gilbert, unpublished).

Kennedy (1951) hypothesized a servo mechanism for speed control as flight heights increased; however, there is no full experimental support for this hypothesis. In additional studies on the effect of striped floor pattern size on flight speed we demonstrated that shortening of the tunnel's transverse stripes also led to higher net uptunnel speeds at low and medium flight heights (Kuenen, unpublished). This is consistent with the moths' response to decreasing stripe width in this study. Given that larger stripes, both longitudinally and laterally, result in slower flight speed we speculate that the reduction in flight speed by OFM males over larger ventral visual cues, may mimic their approach to the perch of a pheromone-releasing female OFM and thus they would slow down to more readily locate her while perched on a leaf or branch surface.

Acknowledgments We thank Sarah Hofer for assistance in rearing insects, making the floor patterns and digitizing the moth tracks. This work was funded in part by funds from the California Pistachio Research Board.

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